GERMINATION OF COMANDRA (SANTALACEAE)

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In all parasitic angiosperms germination corresponds to a brief period of independence from host plants. During this short span of time, when growth is facilitated by nutrients present in endosperm and/or cotyledons, the seedling has an opportunity to establish structural and physiological contact with a host plant. It is a rather precarious transitional period of considerable biological interest. Surprisingly little is known, however, about the seedling stage of many parasites including members of Santalaceae, all of which are parasitic. The following structural details relate to the early establishment of *Comandra umbellata* (L.) Nutt. subsp. *pallida* (DC.) Piehl, as based on seedlings found in loose sand in Lethbridge, Alberta, 18 May 1976.

Seedlings of *Comandra* show exceedingly slender, erect stems with narrow, erect leaves when first emerging from the soil (Fig. 1A). They are difficult to spot among older plants, which normally have numerous sterile, unbranched shoots. About 6 or 7 cm below soil level the entire fruit was still recognizable, the fruit wall turned nearly black, and both it and the hard mesocarp split open on the apical pole. From this pole there protruded the withered endosperm still enclosing the 10 mm long cotyledons, which were separate at the base but closely adnate in the upper one-third (Fig. 1B, 1F). The cotyledons, which were only a fraction of a mm at the time of fruit dispersal (Piehl, 1965), remain in that position until they decay.

The initial stages of germination are clearly described and illustrated by Piehl. The precise origin of roots and rhizomes, however, needs further comment. Piehl states that the first rhizomes originate "in the transition or cotyledon region" of the axis. In my material there was no sign of lateral buds associated with cotyledons, while buds were clearly recognizable in the axils of the first one or two reflexed scale leaves (Fig. 1C). It is thus at this level, several cm below the soil surface, that the rhizomes originate in axillary positions. In several plants axillary roots had also formed in association with both these scale leaves and the cotyledons (Fig. 1C, 1D). Where both a bud and a root are formed in an axillary position, they already show the same regular position with respect to each other that characterizes the mature rhizome system (Fig. 1C; cf. Kuijt, 1969, Fig. 3–6).

Haustoria are formed even two weeks following germination. Many haustoria in the seedling are closely similar to the so-called "haustorial rudiments" that Simpson and Fineran (1970) described for *Mida*. They are rather elongate, spur-like outgrowths clearly continuous with that

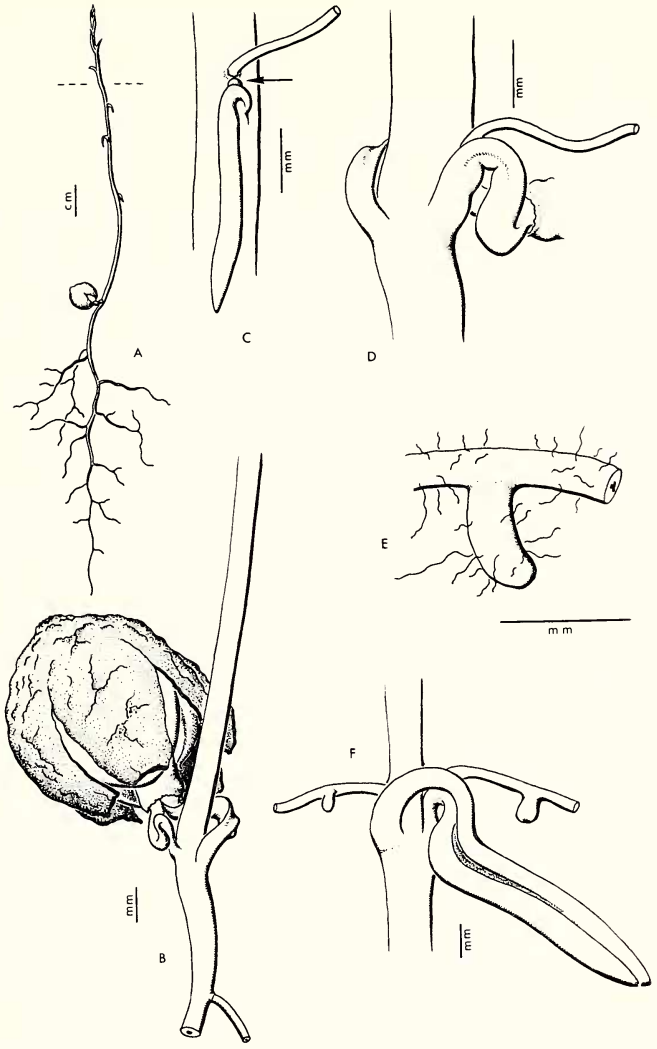

FIG. 1. *Comandra umbellata*. A. Seedling; soil level indicated by broken line. B. Cotyledonary zone. Within the cracked fruit wall the yellowish shell is visible, from which the tubular remnant of the endosperm, containing the twisted cotyledons, protrudes. Compare D and F. C. One of several subterranean nodes, about 4 cm above cotyledons, showing recurved scale-leaf and axillary root, between which is the axillary bud (arrow). The axillary root probably develops into a rhizome. D. Cotyledonary zone, showing twisted cotyledons still in exhausted endosperm, one cotyledon having an axillary root. E. Haustorial "rudiment", 4 mm along first lateral root, 5 mm below cotyledons. F. Cotyledonary zone with endosperm removed, the cotyledon tips cohering. Two axillary roots have formed, each bearing one young haustorium.

of the mother root (cf. Kuijt, 1969, Fig. 5). These rudiments thicken upon contact with host organs, and many eventually differentiate into haustoria. They develop on any root, whether below the cotyledonary node or above it, sometimes only a few mm away from the shoot in the latter cases (Fig. 1F), except for the upper portion of the primary root, which always seems to lack haustoria.

The only other Santalaceae where germination has been described are *Exocarpos* (Stauffer, 1959; Fineran, 1962) and *Santalum album* (Barber, 1906). Both these plants, and quite probably also *Buckleya* (cf. Kusano, 1902) are epigaeous and non-rhizomatous. Because *Comandra* is hypogaeous and rhizomatous it may be predicted that other rhizomatous genera such as *Arjona, Geocaulon, Nanodea,* and possibly *Nestronia* also have a hypogaeous type of germination.

Literature Cited

Barber, C. A. 1906. Studies in root parasitism. The haustorium of *Santalum album*. 1. Early stages, up to penetration. Mem. Dept. Agriculture India, Bot. Ser. 1:1–30.

Fineran, B. A. 1962. Studies on the root parasitism of *Exocarpus* (sic) *bidwillii* Hook. f. I. Ecology and root structure of the parasite. Phytomorphol. 12:339–355.

Kuijt, Job. 1969. The biology of parasitic flowering plants. Univ. California Press, Berkeley and Los Angeles.

Kusano, S. 1902. Studies on the parasitism of *Buckleya quadriala,* B. et H., a Santalaceous parasite, and on the structure of its haustorium. J. Coll. Sci., Imp. Univ. Tokyo 17:1–12.

Piehl, M. A. 1965. The natural history and taxonomy of *Comandra* (Santalaceae). Mem. Torrey Bot. Club 22:1–97.

Simpson, P. G. and B. A. Fineran. 1970. Structure and development of the haustorium in *Mida salicifolia*. Phytomorphol. 20:236–248.

Stauffer, H. U. 1959. Revisio Anthobolarum. Santalales-Studien IV. Mitt. Bot. Mus. Univ. Zurich, No. 213.